Fossil Focus: Ammonoids

De Baets, Kenneth ; Hoffmann, René ; Sessa, Jocelyn A ; Klug, Christian

Abstract: Introduction: Ammonoids (Ammonoidea) are an extinct group of marine invertebrates with an external shell. They were cephalopods, and hence closely related to modern cuttlefish, squid, octopuses and the pearly nautilus. In a non-scientific context, they are commonly called ammonites, but that term really includes only Jurassic and Cretaceous forms in its stricter scientific sense. The Ammonoidea as a whole lived from the Early Devonian to the earliest Palaeogene period, covering a timespan of about 350 million years. Normally, only their shells, also called conchs, or their internal moulds are found in the fossil record. Conchs from adult ammonoids range from about 5 millimetres to 2 metres in diameter. Due to the large diversity (taxonomic richness), disparity (morphological richness), nearly global distribution and abundance of their shells in the fossil record, ammonoids have been valued by geologists, palaeontologists, biologists and fossil collectors alike. They have been particularly useful for studies of biodiversity and for correlating and assigning relative ages to rocks (the field of biostratigraphy). Ammonoids have also proved valuable for studying the processes and patterns of evolution, because they repeatedly evolved towards more coiled, larger and/or more complex conchs. They probably had a large variety of life modes and reproductive strategies, but despite the widespread attention that they have received, there are still several controversies concerning the group's palaeoecology, anatomy and evolutionary relationships.

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by Kenneth De Baets[1], René Hoffmann[2], Jocelyn A. Sessa[3] and Christian Klug[4].

Introduction:

Ammonoids (Ammonoidea) are an extinct group of marine invertebrates with an external shell. They were cephalopods, and hence closely related to modern cuttlefish, squid, octopuses and the pearly nautilus. In a non-scientific context, they are commonly called ammonites, but that term really includes only Jurassic and Cretaceous forms in its stricter scientific sense. The Ammonoidea as a whole lived from the Early Devonian to the earliest Palaeogene period, covering a timespan of about 350 million years. Normally, only their shells, also called conchs, or their internal moulds are found in the fossil record. Conchs from adult ammonoids range from about 5 millimetres to 2 metres in diameter.

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Anatomy:

It is generally rare for soft tissues to be preserved in the fossil record; this is especially true for ammonoids. This could be related to various factors including ammonoids' anatomy (if they had no or very short arms, or only fragile ones, preservation of the arms would be impossible or unlikely). Furthermore, the fact that ammonoids were mobile organisms living within the water column also contributes to the rarity of soft tissue preservation. If gases remained inside their shell after death, the conchs could have continued to float and to be transported, allowing soft tissue to evade rapid burial and thus fossilization. Nevertheless, a few exceptionally preserved specimens have offered insights into some aspects of these molluscs´ anatomy and mode of life.

The first remarkable discoveries of ammonoids with some soft tissues preserved occurred in Carboniferous rocks (between 359 million and 299 million years old) from Uruguay. The tissues in these fossils held in place complete mouthparts, including both upper and lower jaws. The jaws consisted mainly of the material chitin, were probably black, and superficially resembled the jaws of modern cephalopods. Between the jaws was a structure called the radula, which is a tongue-like organ with minute chitinous teeth to grasp and transport food particles (the same structure used by aquatic gastropods to scrape algae off the side of a solid surface). These teeth were arranged in rows, and attached on top of a long, thin ribbon; the tooth rows were lined up across this tongue-shaped structure. At the front edge, they were raised and one row became active. By the Cretaceous period (145 million to 66 million years ago), the mouthparts of many ammonoid groups had already undergone evolutionary changes, reflecting specializations in mode of life, habitat and,

most importantly, diet. The most dramatic changes occurred during the Early Jurassic period, between 201 million and 174 million years ago, when the lower jaw in some groups became split into two shovel-like valves (Aptychus), and covered with the mineral calcite. Accordingly, diversity and disparity was higher in the Jurassic and Cretaceous than during the earlier Palaeozoic era. However, only very few ammonoid radulae have been described so far, so much more preserved mouthpart material is needed to produce a clearer picture of evolution and dietary specializations.

The knowledge of mouthpart shape is complemented by the occasional preservation of stomach contents, which have so far been described only from Mesozoic specimens. These contained planktonic crinoids (sea-lilies), ammonoids, other molluscs (such as bivalves and gastropods), foraminifers (single-celled organisms with tests), crustaceans (ostracods, isopods), sponges and ophiuroids (brittle stars). Some of these prey animals lived on the sediment, while others lived in the water column, suggesting that ammonoids could pick up food items from the sea floor or fish them from the water column. In some cases, ammonoid body chambers have been found to contain conchs and jaws of juvenile ammonoids, sometimes possibly of the same species. There are two interpretations of this: either these ammonoids were occasional cannibals, or the remnants are not stomach contents at all, but offspring, indicating that some ammonoids may have given birth to live young (called oviviparity), which is hard to prove.

Other parts of the digestive tract have been found, including the oesophagus, which is sometimes preserved because it was covered by a thin layer of chitin. Further examples of fossilized soft tissue are the gills, cartilage of the head (possibly with eye capsules), attachment scars from the retractor muscle system responsible for pulling the head into the conch, and two questionable cases of arm relics.

As far as the number, dimensions and shape of arms is concerned, the fossil record has not yet provided specimens that permit a clear answer. Nevertheless, comparison with the relatives of ammonoids gives hints. In evolutionary (phylogenetic) trees, ammonoids stand between the pearly nautilus on one side and cuttlefish, squid and octopuses on the other. The ancestors of cuttlefish and squid (such as belemnites) are occasionally preserved with ten arms. In modern *Nautilus*, the embryo begins with 10 arm buds, which split into +/- 90 arms before the animal hatches. This could mean that ammonoids had ten arms. Hopefully, exceptionally preserved ammonoid fossils might provide evidence supporting or falsifying this hypothesis.

Conch morphology:

The name ammonoid comes from the creatures' shell which is typically coiled in a plane (a shape classified as monomorph) resembling the horns of rams, as often pictured on the head of the ancient Greek god Ammon. There are, however, a great variety of ammonoid conch forms, ranging from tightly coiled, through loosely coiled to uncoiled, irregularly or trochospirally coiled (that is, coiled but not in a plane, like a snail shell). These are called heteromorph shapes. Whatever the shape, the conch of all ammonoids can be subdivided into a body chamber containing the soft parts, and a phragmocone consisting of individual chambers separated by walls called septa and connected by an organic tube called the siphuncle (Figs. 1, 2). The phragmocone of ammonoids and other chambered, now-extinct, cephalopods functioned as a buoyancy apparatus, as in extant *Nautilus* or *Spirula*, and implies a mode of life of floating in the water column. We discuss the questions surrounding ammonoids' habitat further below.

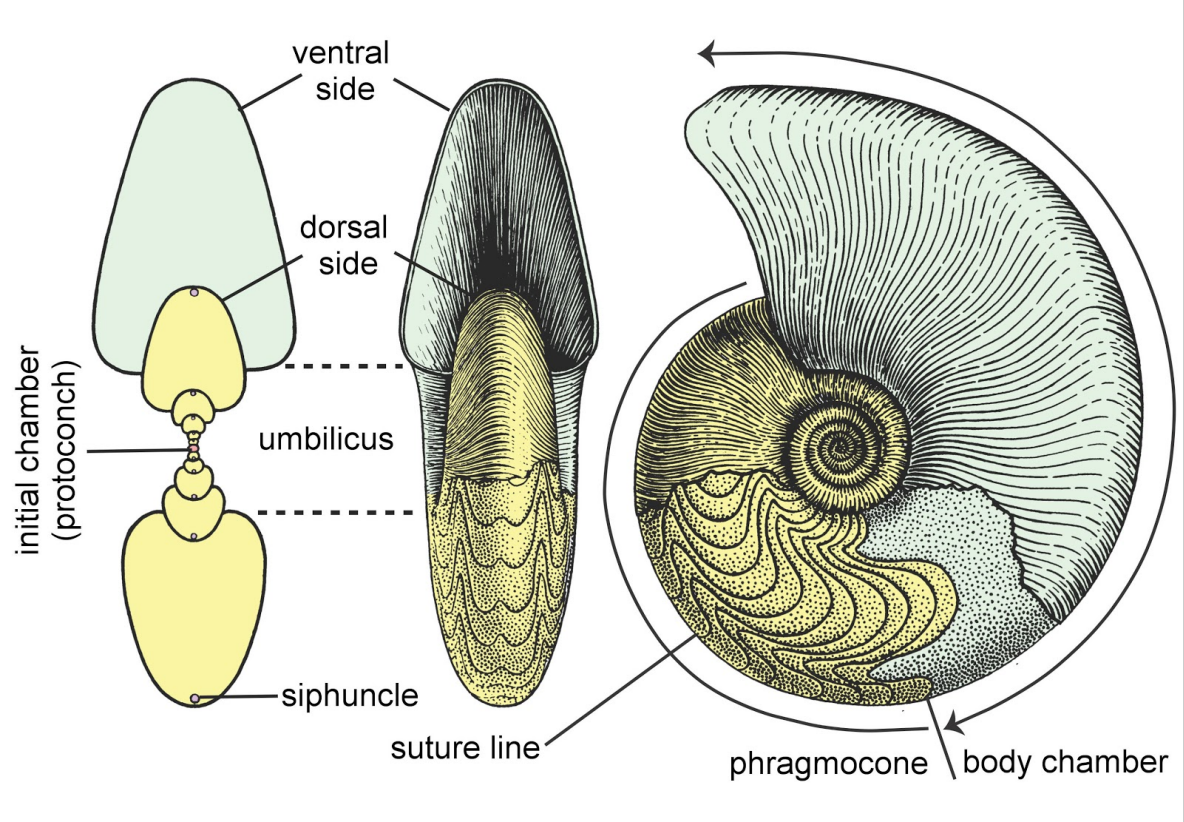

Figure 1 — Morphology and terminology of the ammonoid conch (modified after Arkell 1957; Korn and Klug 2002). Far left showing section across midline.

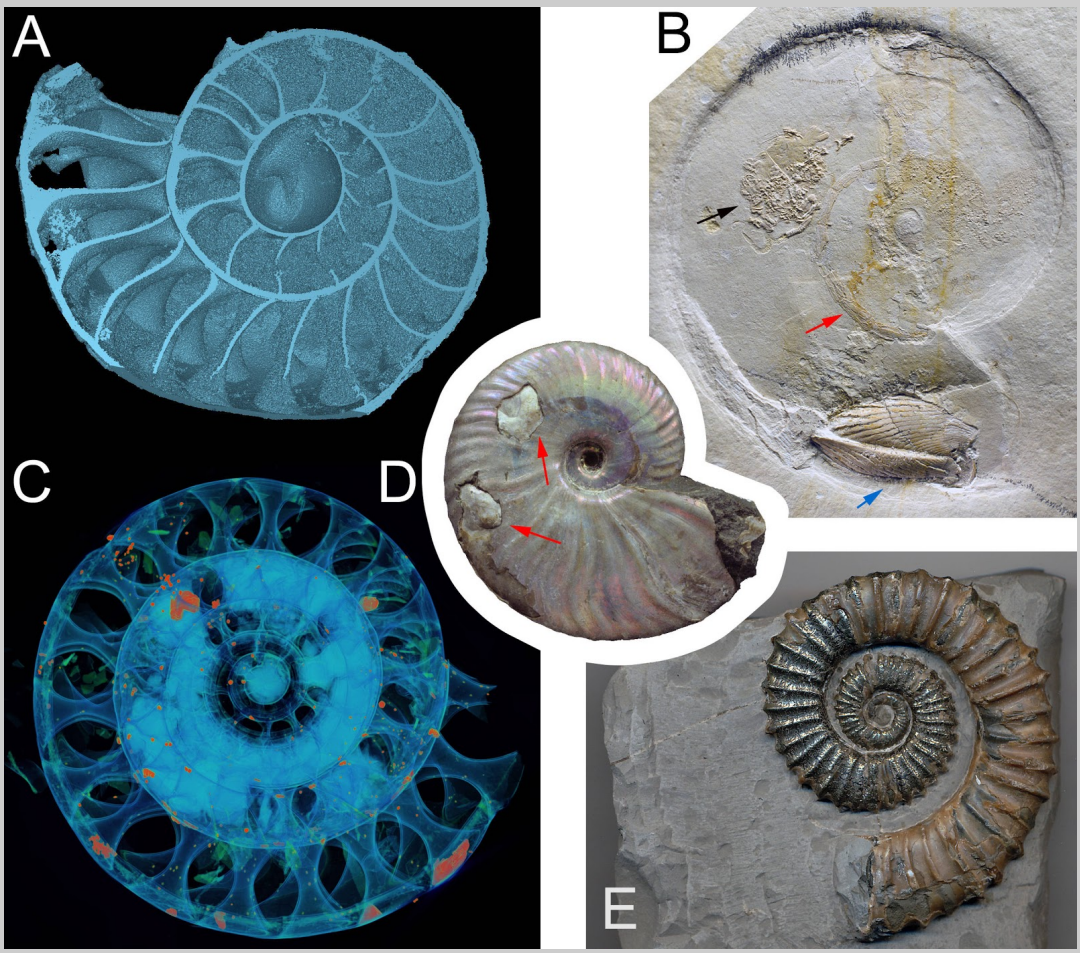

Figure 2 — Internal morphology of the ammonoid conch and specimens showing rare or unusual preservations. A) Juvenile morphology of *Cadoceras* sp. including the initial chamber and the rest of the embryonic shell, reconstructed by Robert Lemanis. B) Jurassic *Neochetoceras* sp. with aptychus at the bottom (blue arrow), parts of the siphuncle (red arrow) preserved and within the body chamber, stomach contents consisting mainly of crinoid remains (black arrow; modified from Keupp 2000). C) CT scan of the Carboniferous ammonoid *Arnsbergites*, reconstructed by René Hoffmann. D) Early Cretaceous specimen of *Cleoniceras besairiei* with injuries attributed to stomatopod crustaceans (red arrows; modified after Keupp 2012). E) Early Cretaceous specimen of the heteromorph ammonoid *Aegocerioceras* housed at the Naturalis Museum in Leiden with complex ammonitic suture lines.

Ecology:

Hypotheses about ammonites' mode of life have often been based on the morphology and strength of their mineralized parts (conchs and septa), as well as the depositional environment (facies) of the rocks they are found in. Based on conch geometry and the thickness of outer shell and septa, the buoyancy of various ammonoids has been calculated, first in the 1940s, using several generalizations and simplifications. Eventually it became clear that the aperture (opening of the body chamber) of species with coiled conchs never faced downwards, and that the orientation of the aperture depended greatly on the length of the body chamber. This is because the body chamber contains the majority of the animal's soft tissues, which have a density similar to that of seawater, whereas the rest of the chambers (phragmocone) are filled with gas, so it is lighter than the body chamber and will float above it. Theoretical buoyancy models have been refined by researchers such as David Raup and Bruce Saunders.

In early research, however, flawed estimates and erroneous simplifications had led to what we now believe to be incorrect assumptions of negative buoyancy (that the animals sank), and to the interpretation that ammonoids lived on or even crawled along the sea floor like gastropods. If this were the case, there should be traces of crawling on the sediment surface — which have not been found. Additionally, there would be no ammonoids in environments with low oxygen at the sea floor, where benthic forms cannot live; however, ammonoids are commonly found in these settings, probably because they in fact lived above the low-oxygen bottom waters. Also, for ammonoids to have crawled on the sea floor, they would have to have had the aperture pointing downwards; yet, if the phragmocone was mostly gas-filled (which most researchers think it was), buoyancy would have turned the aperture away from the sediment surface, i.e. it would have been impossible or at least very difficult for ammonoids to feed on the seafloor.

More recently, reconstructions of ammonoid conchs based on various different methods of tomography have allowed scientists to determine the actual volumes of the conch and gas-filled chambers. All of these empirical models corroborate the hypothesis that an ammonoid shell with only gas in the phragmocone chambers would have floated. If around 20% of the chamber volumes were filled by water, neutral buoyancy could have been achieved. A further argument in favour of the phragmocone being a buoyancy device is rooted in the fact that its construction was refined throughout 300 million years of ammonoid evolution. In the absence of function, the chambered part would have been reduced, as it is in modern squids with alternative means of buoyancy regulation or benthic octopuses.

In the 1970s, shell and septal strength were used to calculate how deep in the water column ammonoids could have descended to without imploding from the pressure of the water around them - at great depth, the surrounding water is much more dense than the gas inside the chambers of the phragmocone (analogous to air inside a submarine). However, these implosion-depth values provide only the depth where implosion would occur; they do not reveal the depths at which ammonites preferentially lived. The deepest record of a living *Nautilus* comes from more than 700 metres depth, yet a *Nautilus* implosion depth of about 800 metres is inferred from mathematical models. Similar mathematical models for ammonoids mostly suggest much shallower implosion depths.

The distance between the centre of gravity and the centre of buoyancy determines the ammonoid's hydrodynamic stability — its stability when swimming, propelled by the water jet out of its funnel. As shown in Fig. 3, the positions of these centres, coupled with the conch shape, are directly related to the orientation of the aperture. Furthermore, the positions of both centres are mainly controlled by the length of the body chamber. During the early evolution of ammonoids, there was a strong evolutionary trend from downwardly oriented apertures to horizontal ones. A more or less horizontal aperture, with the opening facing upwards, was probably the most common, which is reflected in the abundance of Mesozoic species (between 252 million and 66 million years old) with body-chamber lengths of about half a whorl or a 180° volution. Because of the interplay between the centre of gravity and centre of buoyancy, modifications in conch morphology have often been correlated with changes in maximum swimming velocity and manoeuvrability.

Conch geometry and streamlining are important for ammonoids' hydrodynamic properties. One of the most famous models (correct or not) is probably that of Gerd E. G. Westermann, who linked external morphology, both for normally coiled ammonoids and for heteromorph forms, to different modes of life. He suggested that coiled ammonoids were either free-swimming, dwelling towards the bottom of the water column, or floating or drifting within it, whereas heteromorphic ammonoids were planktonic drifters or moved up and down the water column on the basis of their conch shape, orientation and streamlining. However, this is based on a set of ad hoc hypotheses, which might not be true for at least some species. There are several lines of evidence against Westermann's model:

1) Often, ammonoid species have a great variability in conch shape. These different conch shapes, however, are not necessarily linked to a distinct type of environment, based on the rock types in which they are found, and a large range of shapes can occur within a single species found in the same place. Nevertheless, rare studies in which variation has been examined across different environments within the same species indicate that there could be some link; the most frequently occurring variants change with distance from the coast, and with wave agitation. One has to be very careful not to oversimplify things by assuming anything about palaeoenvironment from conch shape alone. There might be a link, but this link needs to be determined from independent evidence.

2) There seems to be a mismatch between conch shapes inferred to be planktonic (and thus living in the water column), and healed injuries attributed to benthic predators (those from the sea floor). As an example, small aperture pits on the conchs of groups such as platycones and planorbicones may have been inflicted by stomatopods (mantis shrimps), consistent with these groups living near the sea floor. By contrast, long slits on groups such as cadicones (*Ptychites*) and serpenticones (*Dactylioceras*, *Subolenekites* and *Pleuroceras*) are attributed to the pincers of crustaceans known as eryonids — also bottom-dwellers — and so inconsistent with a planktonic interpretation for these shapes.

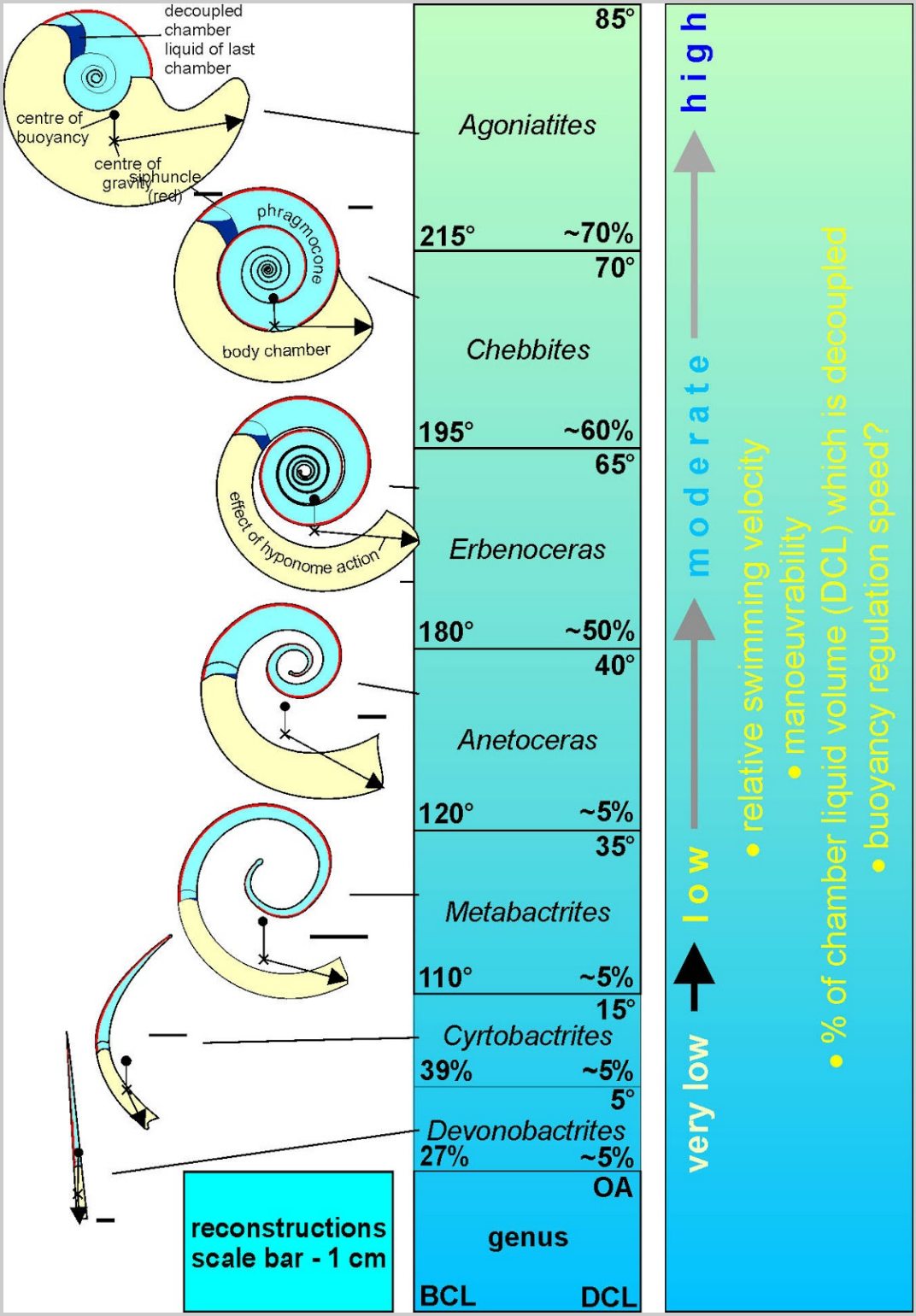

Figure 3 — Evolution of coiled ammonoid shells from straight shells and the consequences for body-chamber length, aperture orientation, thrust angle of the jet they use to move, hydrodynamic stability and interpretations for swimming capabilities throughout evolution; rightmost column shows the evolution of aperture orientation. (Modified after Klug and Korn 2004). BCL, body chamber length; OA, orientation of the aperture; DCL, decoupled chamber liquid.

Furthermore, other types of bite traces on different taxa were probably caused by cephalopods, fish and marine reptiles living between the bottom and the upper part of the water column. This corroborates the hypothesis that different ammonoids lived in different environments, and indicates that although shell geometry sets limits to ammonoid swimming capabilities, it does not necessarily correlate closely with mode of life or habitat.

3) A growing number of studies are using chemical analyses to narrow down ammonoid habitat. In the ocean, the ratio of naturally occurring stable isotopes of oxygen is primarily dependent upon water temperature. Ammonoids incorporate these oxygen isotopes into their calcium carbonate conchs, so the chemical composition of the conch can be analysed to provide palaeotemperature estimates in well-preserved shells which still consist of pristine aragonite. Additionally, because ammonoids accrete shell material as they grow, changes in habitat during life can be detected by sampling the conch through its growth (Fig. 4).

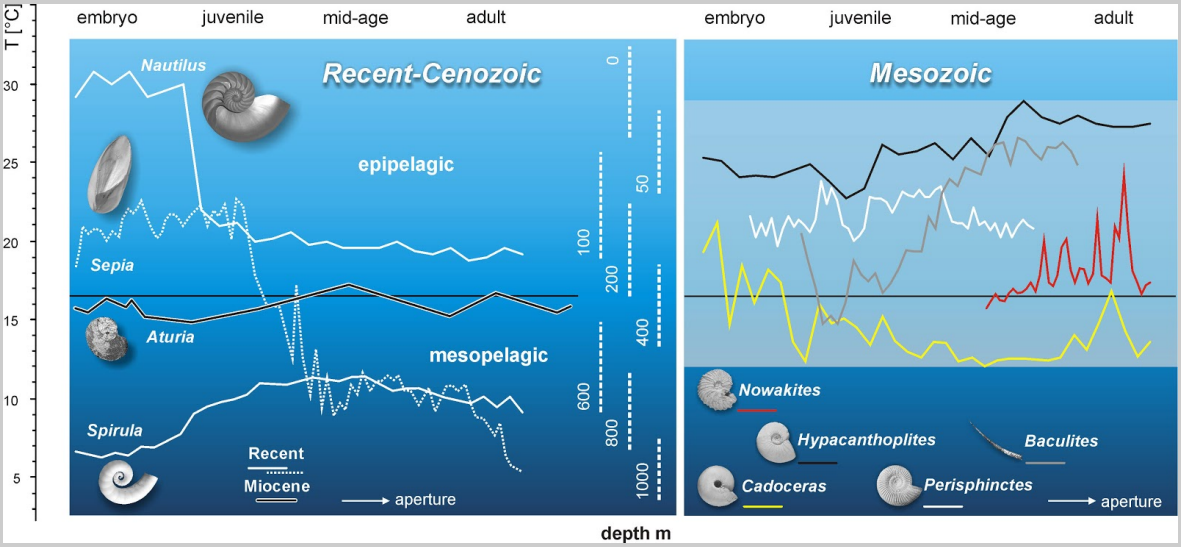

Figure 4 — Habitats and sea water temperature estimated from oxygen isotope data in extant cephalopods (left) and ammonoids (right; modified from Ritterbush *et al*. 2014 and Lukeneder *et al*. 2010).

Many modern cephalopods migrate from shallower to deeper waters (and vice versa) during their lifetime, as well as from close to shore to further from it (and vice versa). They do this on timescales ranging from daily to yearly. These migrations can be related to following a food source, or to currents, seasons, spawning or egg laying. Temperature in the ocean varies latitudinally, and with depth and distance to shore, and so if an ammonoid has migrated, it can be difficult to isolate the temperature signal in its conch, and to tell whether this changed over the lifetime of an individual. To disentangle this, researchers often analyse the oxygen isotopic composition of the ammonoids along with that of organisms found in the same area that lived at known depths and that do not exhibit migratory behaviours. For example, Sessa and colleagues analysed the isotopic composition of three groups of Late Cretaceous (more specifically, latest Maastrichtian: 64.7 to 66 million years old) ammonites, along with that of foraminifers, gastropods and bivalves that lived on the sea floor or buried within it, and that of surface-dwelling planktonic foraminifers. By establishing the temperature of the sea surface from the planktonic foraminifers and the temperature at the sea floor from the benthic foraminifers, gastropods and bivalves, they were able to determine that baculitid and scaphitid ammonites had isotopic values closer to those of the sea-floor organisms, and

therefore probably lived towards the bottom of the water column. By contrast, shells of sphenodiscid ammonites yielded temperatures that were as warm as those measured in planktonic foraminiferan shells, suggesting that they lived in shallower waters than the baculitids (*Baculites*, *Eubaculites*) and scaphitids (*Discoscaphites*). Other studies from the Late Cretaceous have used similar methods, and found that other members of a group called the Ancyloceratina (the suborder containing baculitids and scaphitids) lived just above the sea floor, as did several other ammonoid groups: the Phylloceratina, the Lytoceratina and the Ammonitina.

Other authors have demonstrated significant habitat changes through an individual's growth and development (its ontogeny), which can sometimes be similar to that of extant cephalopods, but can also differ considerably. These habitat changes are often large enough that, through sampling along the direction of conch growth, the oxygen isotopic record of the conch can be used to delineate life stages from embryo to juvenile to adult. For example, important life events, such as reaching sexual maturity, can sometimes be inferred from these habitat changes. One study sampled the Jurassic ammonite *Cadoceras* from the Callovian (ca. 165 million years old) of Russia at a high resolution through ontogeny, and identified a juvenile stage that lived in shallow waters, followed by an adult stage that migrated into deeper waters. The team also inferred spawning behaviour from a sharp rise in temperature (and thus a move to shallower waters) during the adult stage. That some ammonoid groups spent portions of their life in different environments may explain why the juveniles of some species are only found in one setting and the adults are largely or solely found in another.

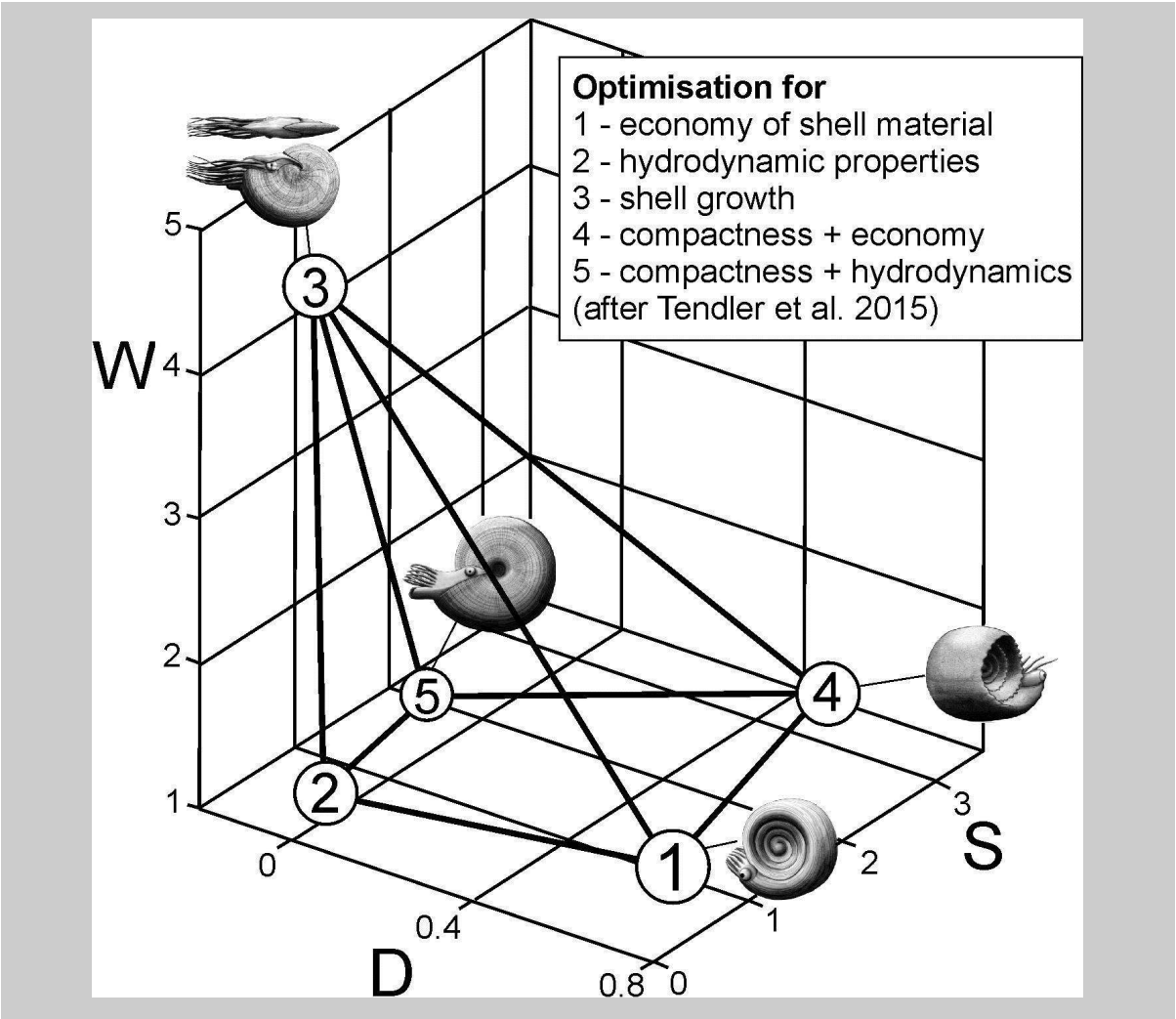

Figure 5 — Ammonoid morphospace after Tendler *et al*. (2015) using the Raupian parameters W, S and D (Raup 1966). W, rate of size increase of the generating curve per whorl; D, distance between the generating curve and the coiling axis; S, shape of the generating curve, equivalent to the cross-sectional shape of the tube (modified after Klug *et al*. 2016).

Another approach to assessing possible functional aspects of conch shape applied a technique called Pareto Optimization to the range of known ammonoid morphologies. The researchers assumed that ammonoid shapes can never fully be optimized for a single function (such as swimming) because of trade-offs between different tasks, including swimming (hydrodynamics), growth and compactness of the conch (a small conch is advantageous because it reduces embryo size, and makes the conch less vulnerable to predator attacks). The distribution of data in Fig. 5 (including increase in the number of whorls, W; umbilical width, D; and whorl cross-section, S) yielded a pyramid with five vortices, each representing one 'archetype'. These archetypes are each optimized for one of the five tasks.

Ontogeny and reproductive strategy:

The ammonite shell grows by continually adding layers of calcium carbonate to the leading edge or aperture of the conch, so that their entire life history is recorded in their shells, from embryo to adult (Fig. 6).

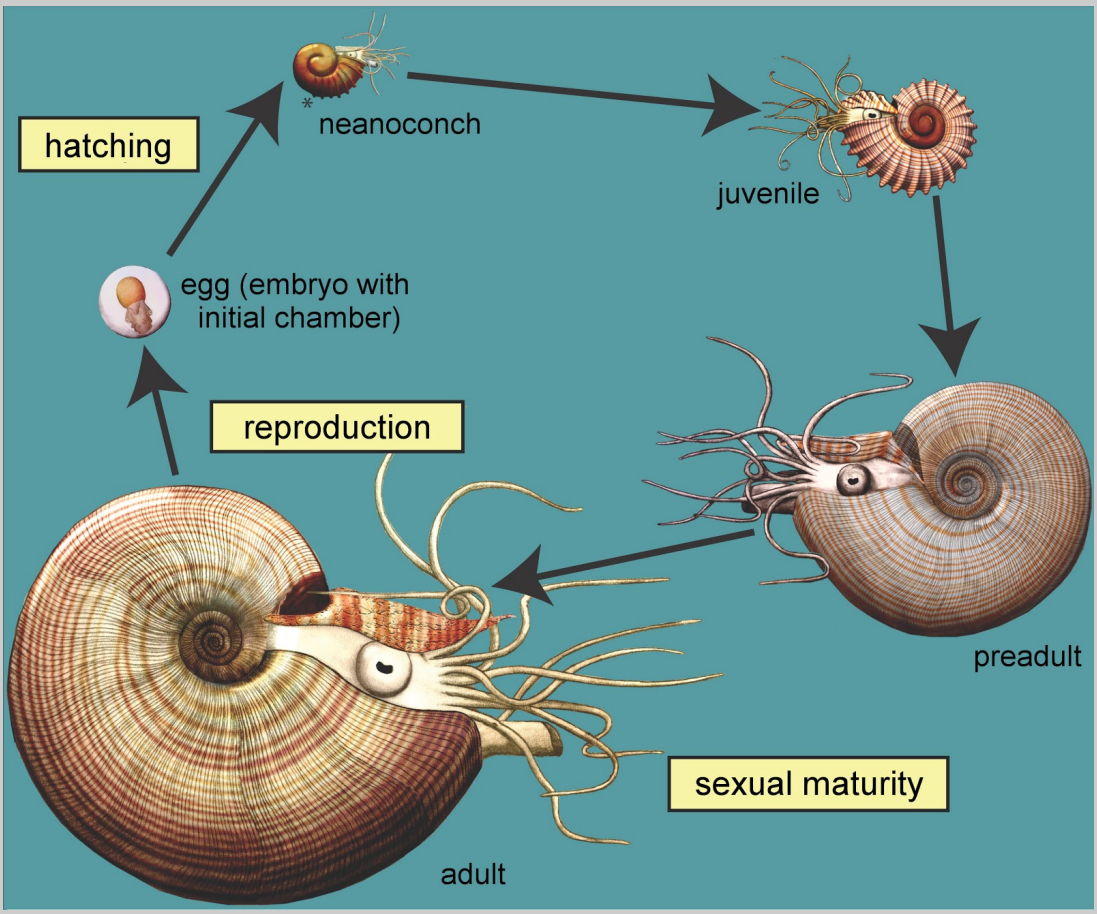

Figure 6 — Life cycle of an ammonoid, exemplified with the Late Devonian genus *Manticoceras*. Modified after Korn and Klug (2007).

Different ontogenetic stages are marked by constrictions, or changes in conch shape, shell thickness and ornamentation. The embryonic conch can be recognized by a discontinuity in growth called the nepionic constriction, which provides a good measure of egg size. Carboniferous and younger ammonoids had a small embryonic conch between 0.5 and 1.5 millimetres across, but in older species, this may be considerably larger — up to 6 mm. During their early evolutionary history, ammonoids rapidly became ever more coiled, reduced the size of their embryonic shell and simultaneously demonstrated a trend towards larger adult size in some groups. Smaller embryos allowed an increase in the number of young they could produce (fecundity). Higher fecundity and mortality of these less primitive ammonoids is supported by small hatchling size and local occurrences of large numbers of preserved embryonic shells in sediments, and also in the intestinal contents of predators. Ammonoid hatchlings are thought to have had a planktonic mode of life, indicated by: buoyancy calculations, their common occurrence in low-oxygen sediments where they are found with planktonic gastropods and little to no benthic organisms (e.g., organisms living on or within the seafloor), and their small size compared to the adults, similar to modern cephalopods that disperse as plankton. The wide distribution of various loosely coiled or trochospirally coiled heteromorphic ammonoids, which are thought to have been poor swimmers, supports the hypothesis of a wide transportation by oceanic currents during a juvenile planktonic stage. Most authors agree that ammonoids laid eggs, but how and where they did so is still unknown (and a recent study suggested that some might have given birth to live young). Their egg-laying habits likely varied between species, ranging from laying eggs on the sea floor to producing floating egg masses or even brood care, as observed in extant cephalopods. This range is also supported by the large variability in ammonoid adult size and shape, as well as differences in the extent of sexual dimorphism (that is, differences in appearance between male and female animals within the same species). In many species, particularly during the Jurassic period, sexual dimorphism was often very pronounced, whereas in others, it seems to have been insignificant or absent.

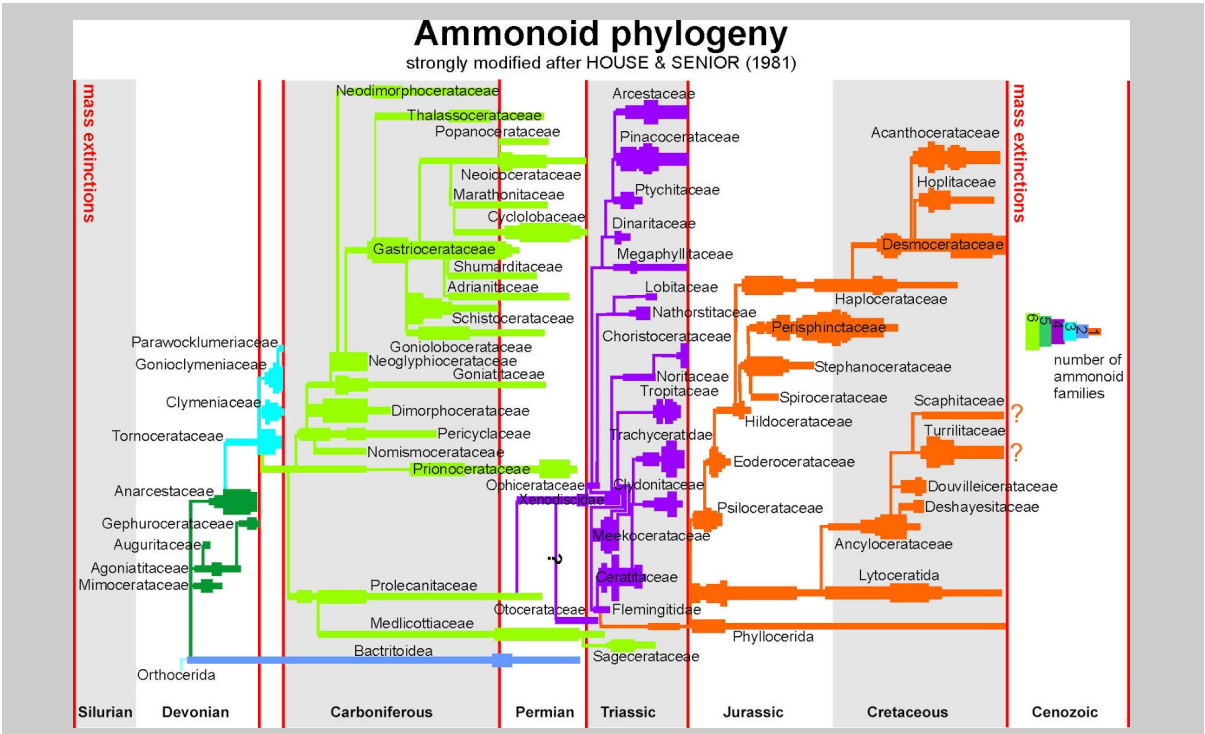

Figure 7 — Origin and diversity of ammonoids and the effects of mass extinctions (modified after Ernst and Klug 2011).

Ammonoid diversification and phylogeny:

The oldest ammonoids come from the Early Devonian period (Emsian: 408 to 393 million million years ago) of Germany, China and Morocco. Ammonoids had a successful evolutionary history, spanning nearly 350 million years, and surviving the Late Devonian, Permian–Triassic and Triassic–Jurassic extinction events (Fig. 7). During these phases of adverse ecological conditions, they went through periods of low diversity, called bottlenecks. Only a few genera survived these mass extinctions, but they rapidly recovered and re-diversified earning them the name of a "boom-and-bust" clade. This has been attributed to their low position in food webs, as well as their reproductive strategy. Early in ammonoid evolution, the embryo size was reduced to about 1 millimetre. Simultaneously, body-chamber volumes increased, allowing a potentially drastic increase in offspring numbers. Early ammonoids laid possibly only around 100 eggs per female, but it is possible that huge Cretaceous ammonites might have produced tens of millions of eggs. Interestingly, both their position in food webs and their reproductive strategy might have contributed to their demise close to the Cretaceous/Paleogene boundary (various new studies indicate that some populations might have survived in the earliest Paleogene or Danian). If marine primary producers (plants and other photosynthesizing organisms) and zooplankton that directly depended on them suffered and declined in the extinction event that killed the dinosaurs — and it seems likely that they did — those groups that fed on them, including ammonoids would also have decreased in diversity and abundance. Furthermore, the minute size of ammonoid offspring (0.5–1.5 millimetres) means that they would have had few reserves to survive even short phases of low food availability, in contrast to the much larger nautilid offspring (10–20 millimetres).

Ammonoids first evolved from animals with straight conical (orthoconic) shells, with simple dome-shaped septa. Translocation of the siphuncle, lateral flattening of the shell tube and increasing conch coiling caused the line of attachment (suture line) of the chamber walls (septa) to become more and more intricately folded as the group evolved (a trend known as suture-line frilling). Palaeozoic ammonoids typically had very simple suture lines called agoniatitic or goniatitic (Fig. 8). By contrast, Triassic ammonoids have more complex ones (ceratitic; only the backward vaulted lobes are serrated). Jurassic–Cretaceous forms have the finely frilled, most complex ammonitic suture lines.

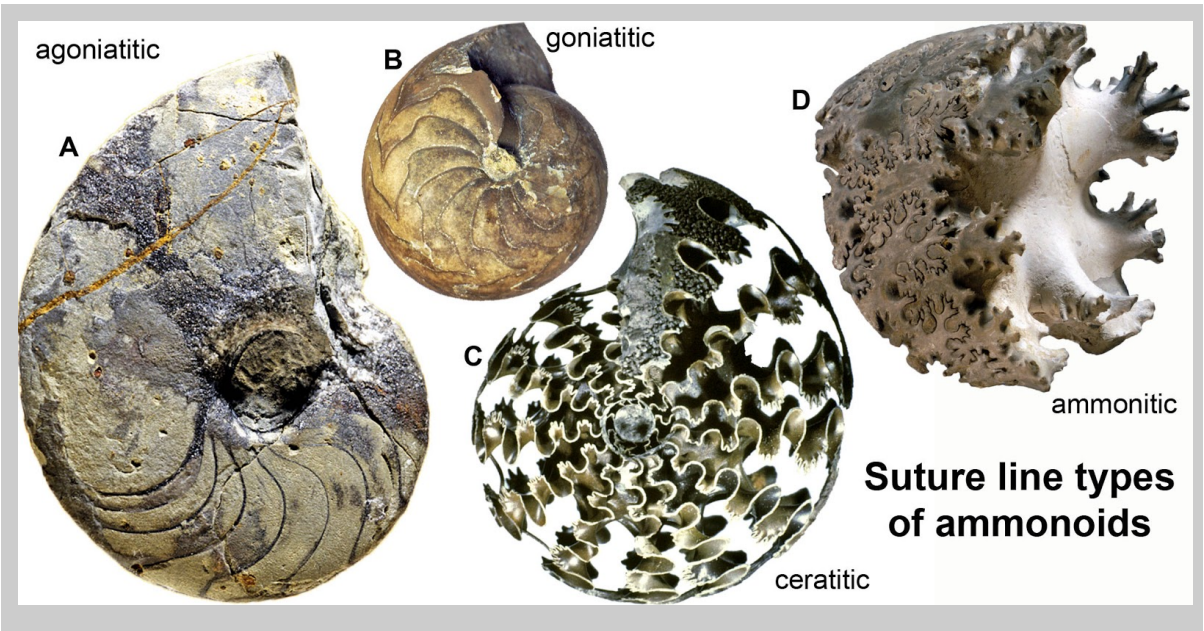

Figure 8 — Sutures and septa of some ammonoids (modified after Klug & Hoffmann 2015: fig. 3.1). A, *Agoniatites vanuxemi* (Hall, 1879), latest Eifelian, Jebel Amessoui, Tafilalt, Morocco; Institut für Geowissenschaften (Tübingen, Germany); diameter 15 centimetres. B, *Goniatites multiliratus* Gordon, 1862, middle Mississippian, Jackfork Creek, S of Ada, Oklahoma (USA); PIMUZ 31257 (Paläontologisches Institut und Museum, Universität Zürich, Switzerland); diameter 43 millimetres. C, *Amphipopanoceras* cf. *medium* (McLearn 1948), SGPIMH no. 3181 (Universität Hamburg, Germany), Triassic, Spitsbergen, Norway; diameter 25 millimetres; acid-prepared specimen with phosphatized septa and siphuncle; from Weitschat (1986). D, *Lytoceras* sp., Aalenian (Jurassic), Heiningen near Göppingen, Germany, whorl height 84 millimetres, Staatliches Museum für Naturkunde Stuttgart, Germany, SMNS 23156 (after Ernst and Klug 2011).

Despite being one of the most-studied fossil groups, the evolutionary relationships (phylogeny) of ammonoids are still not fully resolved (so actually, Fig. 7 should contain many question marks). This is largely because their phylogeny is based on their conchs, which have a limited amount of strongly varying characters (conch morphology, septa, ornamentation).

Nevertheless, a better understanding of conch-shape changes through ontogeny might aid in resolving the group's phylogeny, and at least help to distinguish between superficially similar adult forms. Studying variation within species by using many ammonoid conchs will contribute to understanding the value of characters in assessing evolutionary relationships.

Mythology:

Fossils of ammonoid shells have been known for several centuries and in medieval Europe were thought to be petrified coiled snakes with healing or oracular powers — as a result, they were known as snake- or serpent-stones. The municipal coats of arms of various European towns (Villers-sur-Mer, Whitby, Gosau, Cremlingen, Lüdinghausen, Schernfeld, etc.) contain ammonoids. Their geometric beauty has often landed them on stamps, postmarks and postal stationary. In some regions of Nepal, ammonites, dubbed saligrams, are believed to be concrete manifestations of the gods Vishnu and Shiva.

Summary:

Despite centuries of study, interest in ammonoids has hardly diminished, leaving room for multiple new discoveries. More exceptionally preserved specimens are necessary to better constrain the anatomy of both internal and external soft tissues of ammonoids. Furthermore, new material will allow for quantitative study of their ontogeny and intraspecific variation, which will help to better understand their phylogeny and ecology. Last but not least, ammonoids with malformations or aragonitic shell preservations are often treated as peculiarities by collectors and researchers alike, but the quantitative study of these unusual specimens might contribute considerably to further constraining the group's palaeobiology.

Suggestions for further reading:

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Palaeocast Episode 17: Ammonoid evolution and ecology.

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